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A New and Unusual Aquatic Reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup)

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ABSTRACT

Hypuronector limnaios (n. gen., n. sp.) is a small reptile described from the Late Triassic (Late Carnian) age Lockatong Formation of the Newark basin of New Jersey. It occurs in the laminated, relatively deep-water portions of sedimentary cycles controlled by orbital forcing of climate. *Hypuronector* has uniquely elongated chevrons that give the tail a fin- or featherlike shape. *Hypuronector* was a member of the diapsid family Drepanosauridae, along with *Drepanosaurus, Megalancosaurus, Dolabrosaurus,* and an undescribed form. The tail of *Hypuronector* was probably used for swimming, although the proportionally long legs suggest that this reptile at least occasionally moved about on land.

INTRODUCTION

Some 40 years or more ago there was a large quarry in North Bergen, New Jersey, on the back slope of the Palisades ridge just west of the Hudson River. The quarry had been developed in a hill, a remnant of Triassic age sediments consisting of indurate siltstones and sandstones dipping to the west with the intrusive diabase Granton sill above and the Palisade sill below (fig. 1). The former hill and the quarry were located between a railroad line on the west and Tonnelle Avenue (Routes 1 and 9 or the Bergen Turnpike) on the east, both of which locally follow the strike of the strata. These sediments of the quarry are a part of the Lockatong Formation of the Newark basin portion of the Newark Supergroup (Olsen, 1978), which

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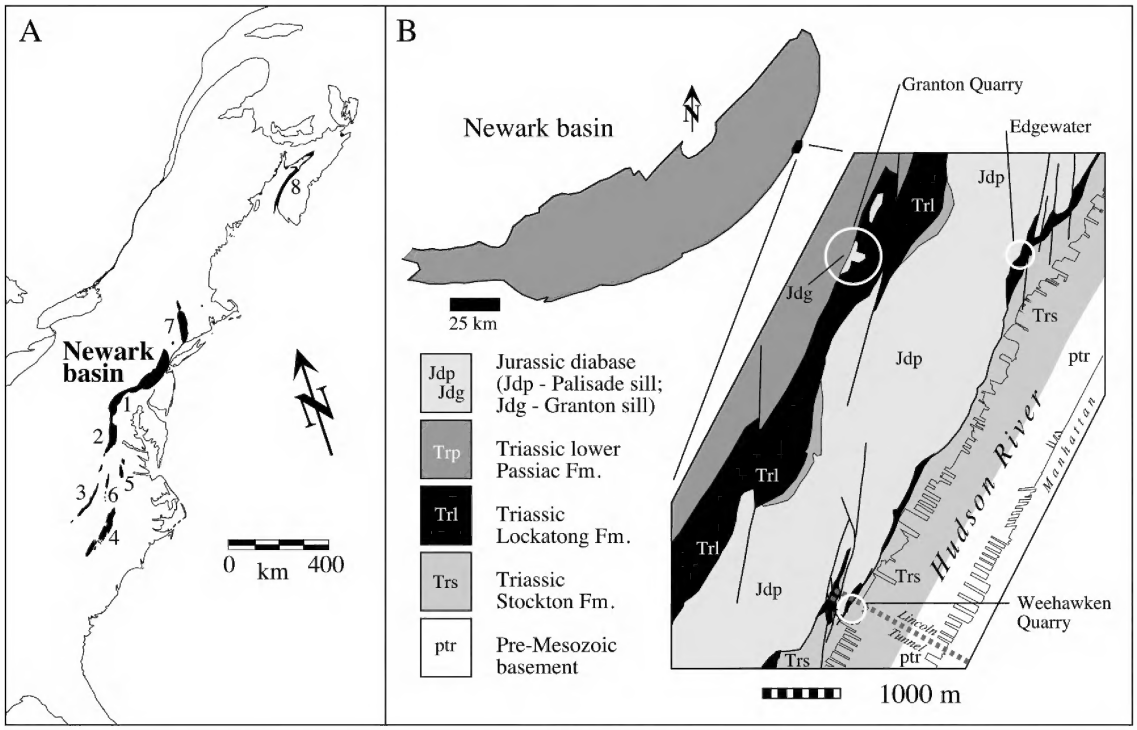

Fig. 1. Location of *Hypuronector limnaios* within the Newark Supergroup (A) and within the Newark basin of the Newark Supergroup (B). **A,** Map of the Newark Supergroup showing the outcropping basins. Major basins other than the Newark basin are: 1, Gettysburg basin; 2, Culpeper basin; 3, Dan River basin; 4, Deep River basin; 5, Richmond basin and associated Taylorsville basin to north; 6, Farmville and associated basins to south; 7, Hartford basin; 8, Fundy basin. Adapted from Olsen et al. (1996). **B,** Detailed map of Weehawken to Edgewater, New Jersey, area showing bedrock geology at major *Hypuronector* localities; based on Olsen (1980), Parker (1993), and Drake et al. (1996).

lies conformably on the sandstones and conglomerates of the Stockton Formation, both being locally intruded by the Early Jurassic Palisade sill that rises so dramatically from the Hudson River along its western shore (fig. 2).

In former years there was a small station known as Granton on the railroad near the quarry and the quarry was commonly referred to by that name. Granton Quarry came to be a frequent stop for both amateur and professional geologists and paleontologists, and eventually, innumerable fossils were collected from the fertile sediments, particularly abundant clam shrimp and the coelacanth fish *Osteopleurus* (*Diplurus*) *newarki* (Schaeffer, 1952).

About a half century ago work began on the demolition of the quarry so that space could be provided for the construction of commercial establishments. Needless to say, the destruction of the quarry was a large undertaking, but it has been carried on to such a stage today that there remains only a small remnant of the hill that once contained the quarry. As a result of this work, however,

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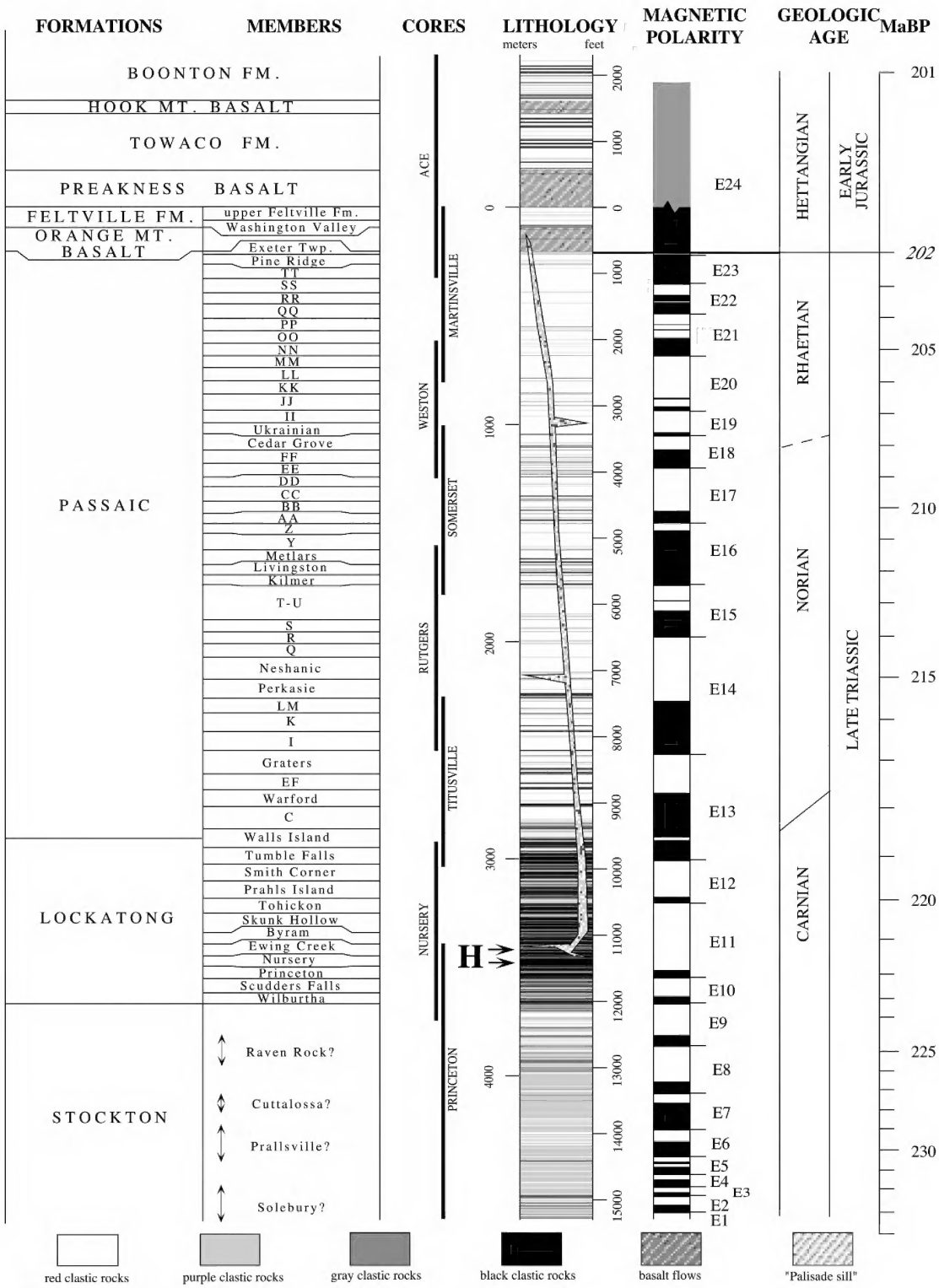
Fig. 2. Stratigraphic section of basin based on the Newark basin coring project showing the temporal and stratigraphic context of the sections containing *Hypuronector* (**H** and adjacent arrows). Adapted from Olsen et al. (1996) and Olsen and Kent (1999).


FORMATIONS
MEMBERS
CORES
LITHOLOGY
meters
feet
MAGNETIC POLARITY
GEOLOGIC AGE
MaBP
BOONTON FM.
HOOK MT. BASALT
TOWACO FM.
PREAKNESS BASALT
FELTVILLE FM.
upper Feltville Fm.
Washington Valley
ORANGE MT. BASALT
Exeter Twp.
Pine Ridge
PASSAIC
TT
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Perkasie
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EF
Warford
C
LOCKATONG
Walls Island
Tumble Falls
Smith Corner
Prahls Island
Tohickon
Skunk Hollow
Byram
Ewing Creek
Nursery
Princeton
Scudders Falls
Wilburtha
STOCKTON
Raven Rock?
Cuttalossa?
Prallsville?
Solebury?
ACE
WESTON
RUTGERS
NURSERY
PRINCETON
MARTINSVILLE
SOMERSET
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E3
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E1
HETTANGIAN
EARLY JURASSIC
RHAETIAN
NORIAN
CARNIAN
LATE TRIASSIC
201
202
205
210
215
220
225
230
red clastic rocks
purple clastic rocks
gray clastic rocks
black clastic rocks
basalt flows
"Palisade sill"

many new fossils were uncovered, notably a skull of a juvenile rutiodontine phytosaur (Colbert, 1965), a gliding lepidosauromorph described as *Icarosaurus siefkeri* (Colbert, 1966), and the aquatic tanystropheid *Tanytrachelos* (Olsen, 1979, 1980). Some of the other fossils that came to light during the protracted destruction of the quarry have yet to be described. Of these, several partial skeletons have proved to belong to a new and bizarre aquatic reptile.

Additional exposures of the Lockatong Formation occur along the base of the Palisades escarpment from Hoboken to Alpine, New Jersey, and like Granton Quarry these outcrops have produced many fossils (Olsen, 1980). A quarry opened for fossils at Weehawken (Olsen, 1980) adjacent to the Lincoln Tunnel, in addition to other exposures to the north, have provided abundant isolated elements of this new reptile. The Granton Quarry skeletons, supplemented with the material from Weehawken, permit the description of most of the skeleton in this paper, the fourth in a series on Triassic tetrapods from the Granton Quarry.

Stratigraphic Relationships and Environmental Context

The Late Triassic (Late Carnian age) Lockatong Formation is a giant, more or less, lens-shaped mass of lacustrine gray, black, and minor red siltstone and sandstone sandwiched between the underlying buff and red clastic rocks of the Late Triassic age Stockton Formation below and the overlying cyclical predominantly red clastic Passaic Formation of Late Triassic to earliest Jurassic age (Van Houten, 1969; Olsen et al., 1996). There are six other formations in the Newark basin above the Passaic as shown in figure 2 and these are of Early Jurassic age (Olsen et al., 1996).

Reaching a maximum thickness of over 1100 m and covering an area of over 7000 km^2, the Late Carnian age Lockatong Formation is the largest gray and black unit in the entire Newark Supergroup. Like most lacustrine portions of the Newark, the Lockatong Formation is composed entirely of repetitive sedimentary cycles caused by the rise and fall of lakes controlled by climate changes governed by celestial mechanics. These are called Van Houten Cycles after the author who first described them from the Lockatong Formation (Van Houten, 1964, 1969). Recent work has affirmed Van Houten's contention that these cycles had a roughly 20,000 year periodicity (Van Houten, 1964; Olsen and Kent, 1996, 1999). As in the rest of the Newark section, each of these Van Houten Cycles can be divided into three lithologically defined divisions. Division 1 consists of laminated to massive gray to red clastics to dolostones with occasional stromatolites, oolites, reptile footprints, some desiccation cracks, ripples, and immature root zones. Division 2 is a thinly bedded, laminated to microlaminated (laminae < 1 mm) red, green or gray to black, sometimes organic-carbon-rich siltstone, claystone, or carbonate showing few or no signs of desiccation. In its best-developed form, division 2 is black and microlaminated and contains abundant and well-preserved fossil fish, arthropods, and small reptiles—including the new form we are describing. Division 3 is a laminated to massive gray to red calcareous clastic unit usually showing abundant signs of desiccation. Tetrapod footprints and root zones are often present as well as carbonate and zeolite-filled fenestral fabrics, and there can also be zones of pseudomorphs after evaporitic minerals. Divisions 1, 2, and 3 represent deposition by transgressive, high-stand and regressive, and low-stand deposits, respectively. Results from scientific coring of the Newark basin show that individual Van Houten Cycles of the Lockatong can be traced over the extent of the formation (Olsen et al., 1996).

In the Newark basin, the expression of Van Houten cycles is modulated by several larger scale cycles which are termed the short modulating cycle ($\sim$100,000 years), the McLaughlin cycle (404,000 years), and the long modulating cycle ($\sim$1.75 million years). Van Houten cycles containing a division 2 that is fossil-rich and microlaminated are found most often in the peaks of the short modulating, McLaughlin, and long modulating cycles. Conversely, in the troughs of these thicker sequences, Van Houten cycles tend to be red and have only a poorly laminated division 2. The 404,000-year McLaughlin cy-

cles are used as mappable members of the Lockatong and Passaic formations, and provide the formal nomenclatural and stratigraphic context into which our new little reptile fits (fig. 2).

In the middle of the Newark basin, such as the area along the Delaware River, Van Houten cycles are about 5–6 m thick, the short modulating cycles tend to be about 25 m thick, McLaughlin cycles are about 100 m thick, and the long modulating cycles tend to be about 440 m thick (Olsen, 1986). However, all of the exposures at which our new reptile was found occur along the northeastern terminus of the Newark Basin, along the Hudson River (fig. 1). This area is close to the hinge margin of the Newark basin half graben, and the thicknesses of all of the cycles are much reduced, with Van Houten cycles averaging about 1.5 m and the short modulating cycles averaging about 7 m (Olsen, 1980; Olsen et al., 1996). Only the Princeton, Nursery, and Ewing Creek members of the Lockatong Formation are recognized in the region of the basin along the Hudson River, and they are intruded by the Palisade sill and related diabase bodies. Hence, the sediments are metamorphosed to varying degrees to hornfels (Van Houten, 1969). Despite the metamorphism, the cycles in this area are much more fossiliferous than their equivalents in the center of the basin, probably reflecting the proximity of the shoreline and uplands.

Eleven Van Houten Cycles are currently visible on the small hill that remains of Granton Quarry, and judging from photographs of the site when the quarry was being destroyed no more than 11 cycles were ever exposed (figs. 3–5). The base of the section seems to be about 38 to 46 m above the upper contact of the Palisade sill, which in this area seems to intrude the Stockton-Lockatong contact. The top of the section is capped by the Granton sill, itself apparently an offshoot of the Palisade sill. Each division 2 of all the cycles at Granton Quarry is sufficiently lithologically distinct from the others that most specimens of the new little reptile can be placed in the quarry section. In addition, we have found specimens in situ in cycle G2. Forms found in the same beds as our new reptile at Granton Quarry include abundant conchostracans and darwinulid ostracodes, the paleonisciform fishes *Turseodus* and *Synorichthys,* the coelacanths *Osteopleurus* (*Diplurus*) *newarki* and *Pariostegeus,* the tanystropheid reptile *Tanytrachelos,* and the gliding lepidosauromorph *Icarosaurus.* Division 3 of at least one cycle (?G7) produced the skull of a juvenile phytosaur (Colbert, 1965). The provenance of the fragmentary metoposaurid amphibian (AMNH uncatalogued) from the quarry is unknown. The distribution of taxa within the Granton section is shown in figure 5.

The Granton Quarry section and the central portion of the Lockatong have not been definitively correlated. Taking the underlying sequence into account, the best match is with Ewing Creek Member of the formation (fig. 2) (Olsen et al., 1996)

In contrast to the western slope of the Palisades ridge, where exposures of the Lockatong are so rare that the tracing of beds laterally is essentially impossible, good exposures of the Lockatong are surprisingly common along the east face of the ridge, below the sill. As a result, lateral correlation of individual cycles along strike for 15 km has been accomplished. Fourteen Van Houten cycles have been traced from northern Hoboken to Alpine, New Jersey (Olsen, 1980) (these are labeled in fig. 5). Cycle W-5 is the only unit in these sections that produces the new little reptile. However, this reptile has been found at three localities, always in the same 3 cm thick bed, with the most distant localities separated by more than 6 km (fig. 1). All of the cycles below the Palisade sill are within 35 m of the Stockton-Lockatong contact, and therefore the stratigraphic position of cycle W-5 lies below all of the Granton Quarry cycles.

Because of relatively good exposure, correlation of individual units below the Palisade sill to members of the Lockatong Formation in the central Newark Basin is far more certain than the in Granton section. There is a clear one-to-one match between cycles in exposures of the Weehawken area to the those in the type Nursery Member core and the cycles in more distant exposures to the southwest (Olsen et al., 1996).

In 1978 a quarry for fossil fishes was opened up in cycles W-5 and W-6 at Kings Bluff in Weehawken, New Jersey, just south

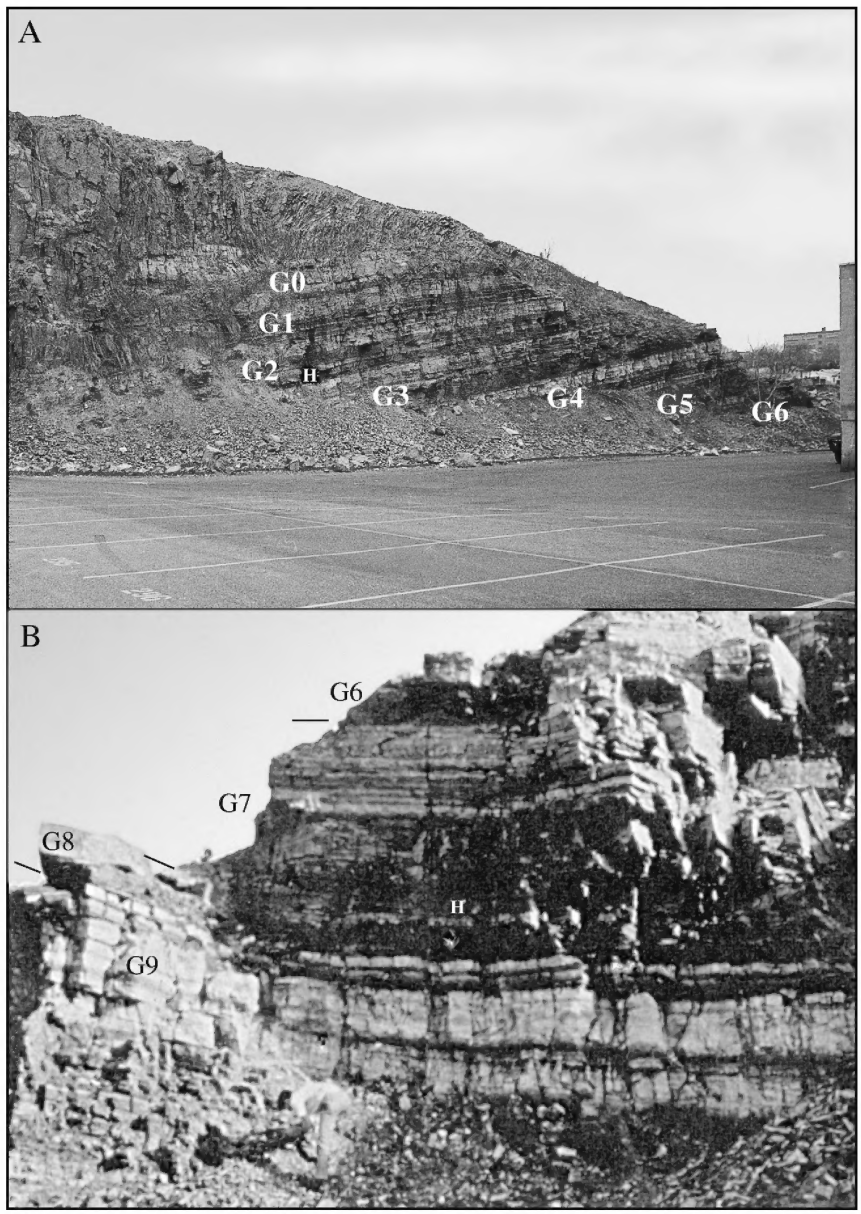


Fig. 3. Ewing Creek (?) Member of the Lockatong Formation of the Granton Quarry and the Granton diabase sill, North Bergen, N.J. **A,** South side of existing hill capped by Granton sill, as it appeared in 1979. Sill is markedly discordant on the left; G0–G6 are cycle designations, and H shows the position of an in situ *Hypuronector* specimen (photo by P. Olsen). **B,** North side of same hill showing cycles G6–G8; H marks the probable horizon of the holotype near the base of cycle G7 based on lithological similarity (photo by David Stager, from Colbert, 1965). All of these units are still currently exposed.

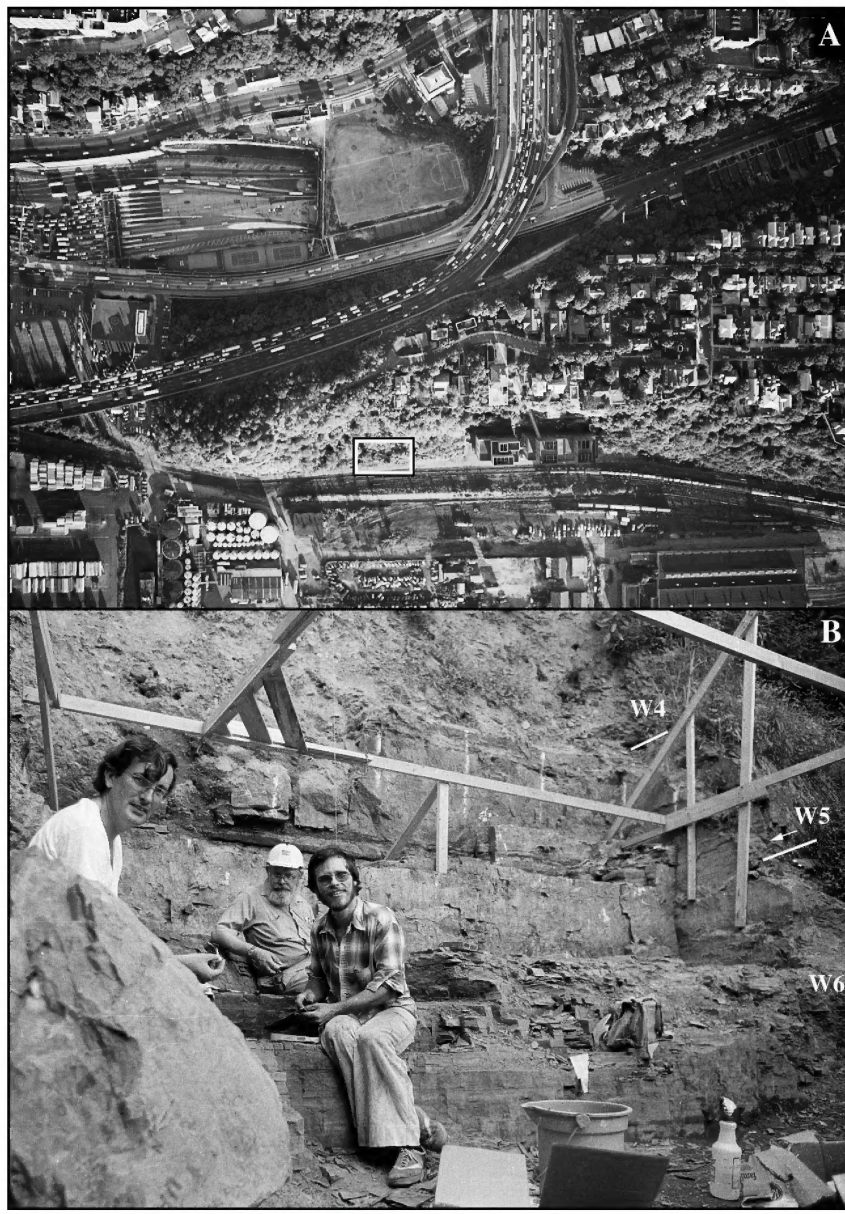


Fig. 4. Weehawken Quarry in Nursery Member of Lockatong Formation. **A,** Aerial photograph of Kings Bluff area, Weehawken, N.J. showing the location of the Weehawken quarry (box), opened for Lockatong vertebrates; illumination is from the bottom (east) during morning rush hour (photo courtesy William K. Sacco, 1978). **B,** The Weehawken Quarry in 1979 showing three cycles of the Nursery Member, including cycle W5 that produced abundant disarticulated *Hypuronector* (arrow) (photo courtesy of Amy R. McCune, 1979); people are, from left to right, Keith Stewart Thomson, Donald Baird, and Paul E. Olsen.

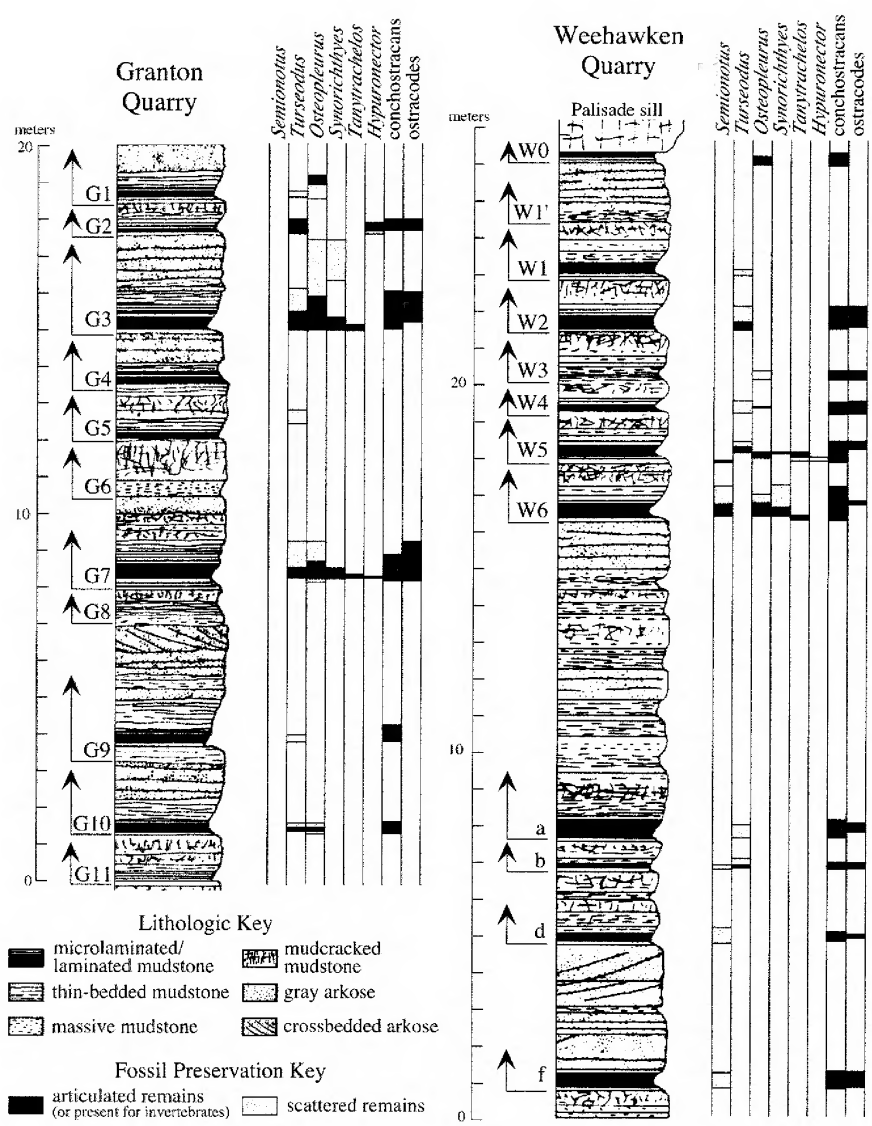


Fig. 5. Measured sections at Granton Quarry and the Weehawken quarry at Kings Bluff showing the distribution of various taxa including *Hypuronector* (modified from Olsen, 1980).

of the western ventilation building for the Lincoln Tunnel on the east face of the Palisades (Thomson, 1979; Olsen, 1980; McCune et al., 1984). In addition to thousands of fish and excellent skeletons of *Tanytrachelos* from both cycles, cycle W-5 produced about 300 mostly isolated elements of this new form. Only a handful of elements have been found at the other two localities. In addition to clam shrimp and ostracodes, other vertebrates from Lockatong Formation localities beneath the Palisade sill include the fishes *Turseodus* spp., *Synorichthyes* sp., *Osteopleurus* (*Diplurus*) *newarki* and *Parioste-geus,* and the holostean *Semionotus braunii* (Gratacap, 1886; Olsen, 1980). Reptiles other than that described here include *Tanytrachelos,* phytosaur scraps, and indeterminate footprints.

The great lateral extent of the microlaminated portions of individual Van Houten cycles in the Nursery Member, as well as in other parts of the Lockatong, strongly suggests deposition in deep (+80 m) very large

(+7000 km^2) perennially stratified lakes (Olsen, 1985). The little reptile we describe here apparently lived along the shores of this great lake when it was at or near its maximum depth. We cannot tell if it also lived in the lakes when they were much shallower or even playas, because vertebrate bones are generally too rare in the less well-laminated divisions 1 and 3.

Institutional Abbreviations: **AMNH,** American Museum of Natural History, New York, Vertebrate Paleontology Collection; **GR,** Ruth Hall Museum of Paleontology, Ghost Ranch, NM; **MCSNB,** Museo Civico di Storia Naturale "E. Caffi", Bergamo, Italy; **YPM,** Yale Peabody Museum, New Haven, CT, Vertebrate Paleontology Collection.

SYSTEMATICS

CLASS REPTILIA LAURENTI 1768

SUBCLASS DIAPSIDA OSBORN 1903

?ARCHOSAURIFORMES GAUTHIER ET AL. 1988

FAMILY DREPANOSAURIDAE OLSEN AND SUES, 1986

REVISED DIAGNOSIS: *Drepanosaurus* (Pinna, 1980, 1984, 1986, 1987; Renesto, 1994a; Renesto and Paganoni, 1995), *Megalancosaurus* (Calzavara et al., 1980; Renesto, 1994b), *Dolabrosaurus* (Berman and Reisz, 1992), and *Hypuronector* (described below) have the following shared derived characters, providing a diagnosis of this diverse family, modified principally from Berman and Reisz (1992). Small diapsid reptiles. Vertebrae with zygophyseal facets generally set very close to midline in the postcervicals; caudal vertebrae with anteroposterially elongated bladelike transverse processes through most of tail and with prezygapophyses of proximal caudals extending anteriorly well beyond centrum and postzygapophyses extending posteriodorsally from neural spine base; neural spines unusually long; at least posterior dorsal ribs very strongly attached or fused to centra; hemal arches or chevrons fused to posterior part of the anterior three-quarters of caudal vertebrae and much greater in depth than height of neural spines; pectoral girdle with high and rodlike scapula; pelvic girdle with high, anteriorly directed blade of ilium.

INCLUDED GENERA: *Drepanosaurus* Pinna 1980, *Dolabrosaurus* Berman and Reisz 1992, *Megalancosaurus* Calzavara, Muscio, and Wild 1980, and *Hypuronector,* described below.

Hypuronector, new genus

Figures 6–14

TYPE AND ONLY SPECIES: *Hypuronector limnaios,* new species

ETYMOLOGY: From the Greek ηψπο (hypo), deep; υρο (uro), tail; νεκτορ, (nektor), the swimmer, meaning the "deep tailed swimmer", the new reptile's informal name for more than 20 years. Name suggested by Donald Baird.

DIAGNOSIS: Small (<18 cm) drepanosaurid with uniquely deep tail consisting of extremely elongated chevrons or hemal spines and proximally high neural spines; the longest hemal spine being equivalent in length to 11 articulated caudal vertebrae. Limbs long and slender; humerus equal to femur in length, radius and ulna about two-thirds length of humerus and longer than tibia and fibula. Differs from *Megalancosaurus* in having notochordal centra and a distally edentulous lower jaw and lacking the peculiarly enlarged anterior dorsal neural spines. Differs from *Dolabrosaurus* and *Megalancosaurus* in lacking the distally expanded tips of the neural spines. Differs from *Megalancosaurus* in having amphicoelous rather than procoelous vertebrae. Differs from *Drepanosaurus* in showing greater fusion of the ribs to the centra, lacking the extreme enlargement of the ungual phalanx digit II of the manus and the greatly broadened ulna, and lacking the "spine" on the tip of the tail. Differs from both *Drepanosaurus* and *Megalancosaurus* in lacking massively enlarged neural spines in the shoulder region and the fenestrate or bifurcate proximal chevrons.

Hypuronector limnaios, new species

Figures 6–14

HOLOTYPE: AMNH 7759, a partially articulated skeleton lacking the skull (fig. 6). Most vertebrae, present including 11 presacrals, two possible sacrals and 38 caudals in close articulation, numerous ribs, shoulder girdle, forelimbs, pelvis, both femora, left tibia and fibula, distal ends of right tibia and fibula. Both pedes and manus incomplete.

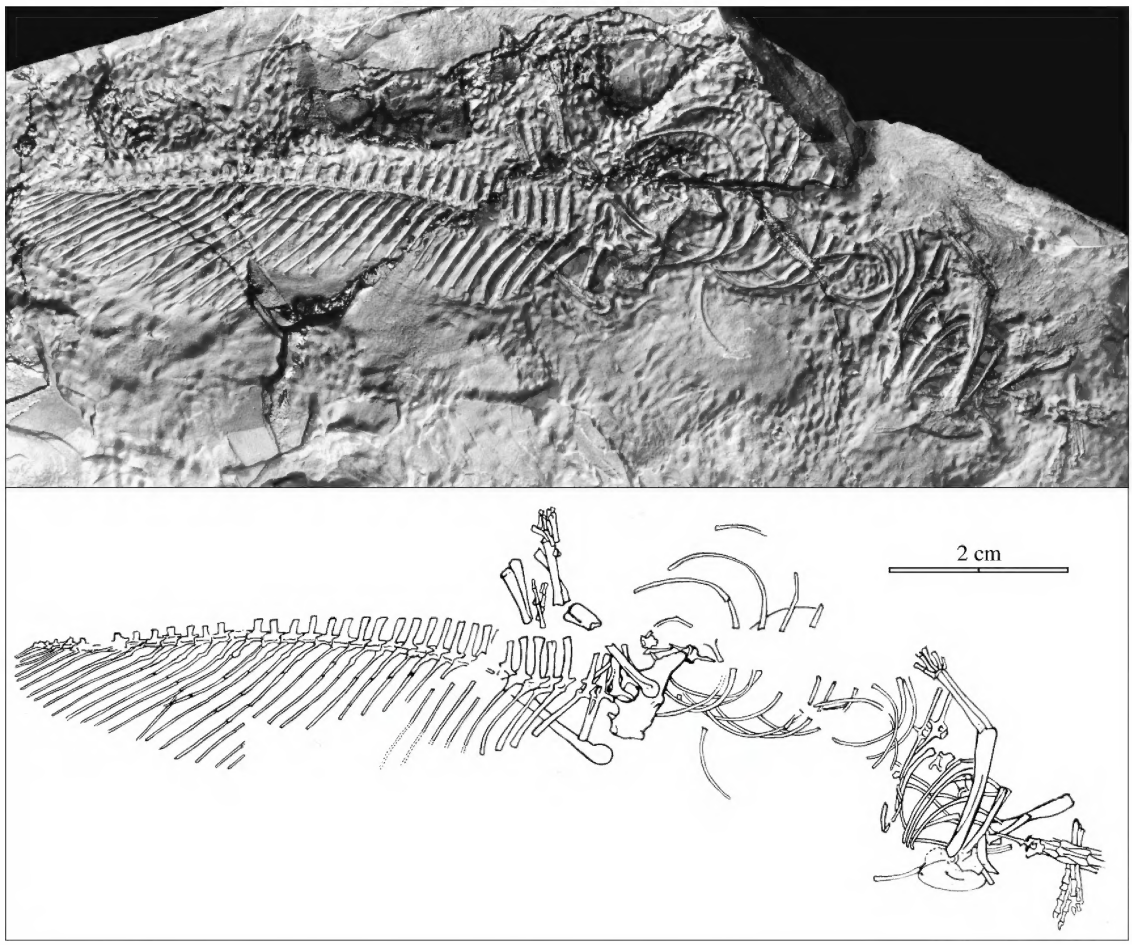


Fig. 6. Holotype of AMNH 7759 (above) and drawing of holotype (below). Photograph by Chester Tarka.

The holotype was prepared by the air abrasive technique.

ETYMOLOGY: Greek λιμναιοσ (limnaios), of the lake, referring to the lacustrine environment in which the animal lived.

REFERRED MATERIAL: From the Granton Quarry: AMNH, 1721, anterior thoracic region including pectoral girdle; AMNH 7205, 5 presacral ribs, fragments of a pelvis, and 13 anterior caudal vertebrae; AMNH 7755, 3 cervical vertebrae, AMNH 1998, 7 caudal vertebrae; AMNH 2080, a dentary with 7 teeth; AMNH 2076, vertebrae; NJSM 19701, partial mostly articulated posterior trunk and anterior tail; NJSM 19702, proximal caudal vertebra and chevron. From Weehawken: YPM 8641, proximal caudal vertebra and chevron; YPM 56385, limb bone; YPM 56386, distal end of humerus; YPM 56387, caudal vertebrae with chevron and ?humerus; YPM 56388, left mandible; YPM 56389, caudal vertebra and partial chevron; YPM 56390, three associated caudal vertebrae with chevrons; YPM 56391, obliquely preserved caudal vertebra and partial chevron; YPM 56392, isolated sacral vertebra; YPM 56393, isolated forelimb. All of the Granton material has been prepared by air abrasion or left unprepared, while all of the Weehawken material has been negatively prepared with hydrochloric acid.

HORIZON AND LOCALITY: Lockatong Formation of the Newark basin portion of the Newark Supergroup, Late Triassic. The ho-

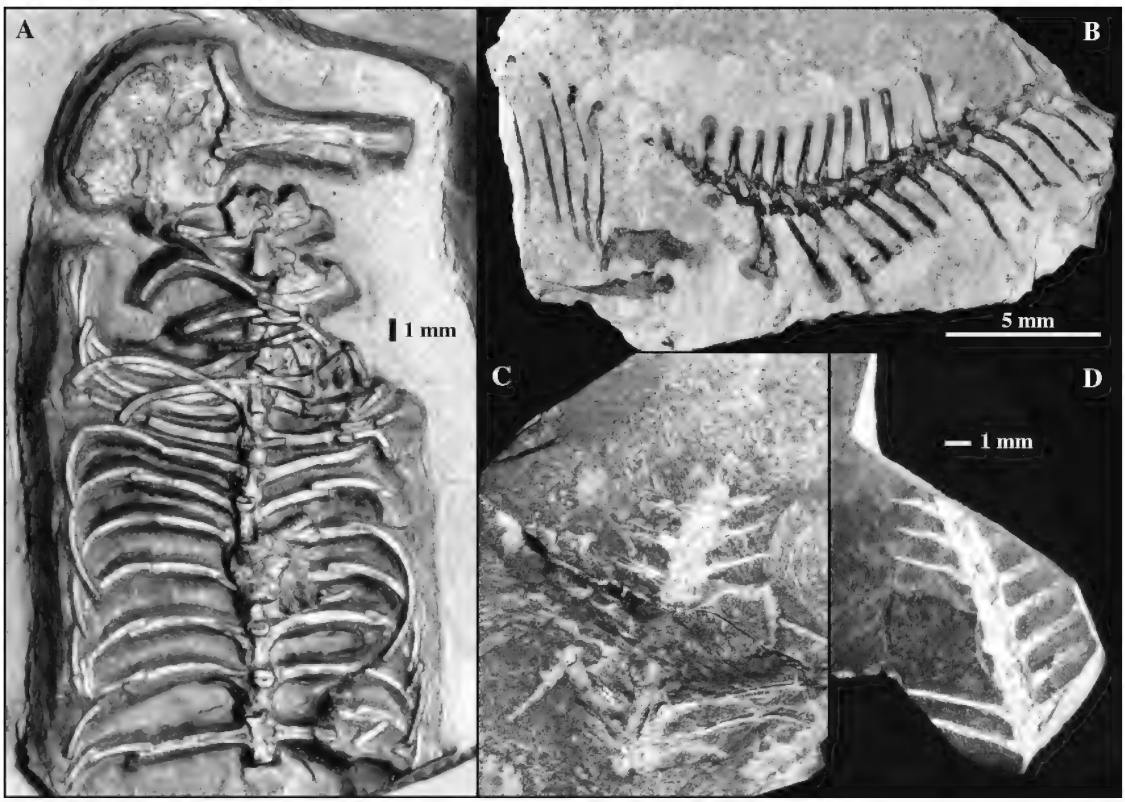


Fig. 7. Additional Granton Quarry specimens of *Hypuronector.* **A,** AMNH 1721, ventral view of trunk and left lateral view of crushed pectoral girdle. **B,** AMNH 7205, partial trunk, pelvic girdle, and proximal caudal vertebrae. **C** and **D,** AMNH 1998, unprepared part and counterpart of midcaudal vertebrae. Photographs by Chester Tarka, except for C and D by Julius Weber (courtesy of G. Case).

lotype is from the Granton Quarry, North Bergen, New Jersey, ?Ewing Creek Member, cycle "G7". Other referred specimens from the Granton Quarry are also from the Ewing Creek Member. Those from Weehawken, New Jersey, are from cycle W-5 of the Nursery Member.

DIAGNOSIS: As for genus, which has only one known species.

DESCRIPTION AND DISCUSSION

SKULL: It is most unfortunate that a skull was not found with the skeleton comprising the holotype of *Hypuronector limnaios.* The specimen is preserved in a thin slab of black shale, which is broken near the front edge of the skeleton. A protracted search was made at the Granton quarry in an effort to find a matching slab that might contain the skull, but to no avail. Curiously, no cranial material has been found associated with the many additional referred specimens.

MANDIBLE: Two isolated mandibles, one from Granton (AMNH 2080) and the other from Weehawken (YPM 56388) have been found associated with unambigous *Hypuronector* material (fig. 8). The mandible is long and shallow with at least six, simple, pointed teeth with possibly pleurodont or subthecodont implantation. The overall shape of the mandible is similar to that in *Megalancosaurus,* however, in both mandible specimens of *Hypuronector,* the anterior half is edentulous. Because, the jaws are very small and crushed, interpretation of sutures is uncertain, however, a primitive reptilian compliment of bones is visible including a dentary, elongate angular, and small surangular; an articular appear present, along with a possible splenial. A small coronoid process is evident, as is a long meckelian groove, medially.

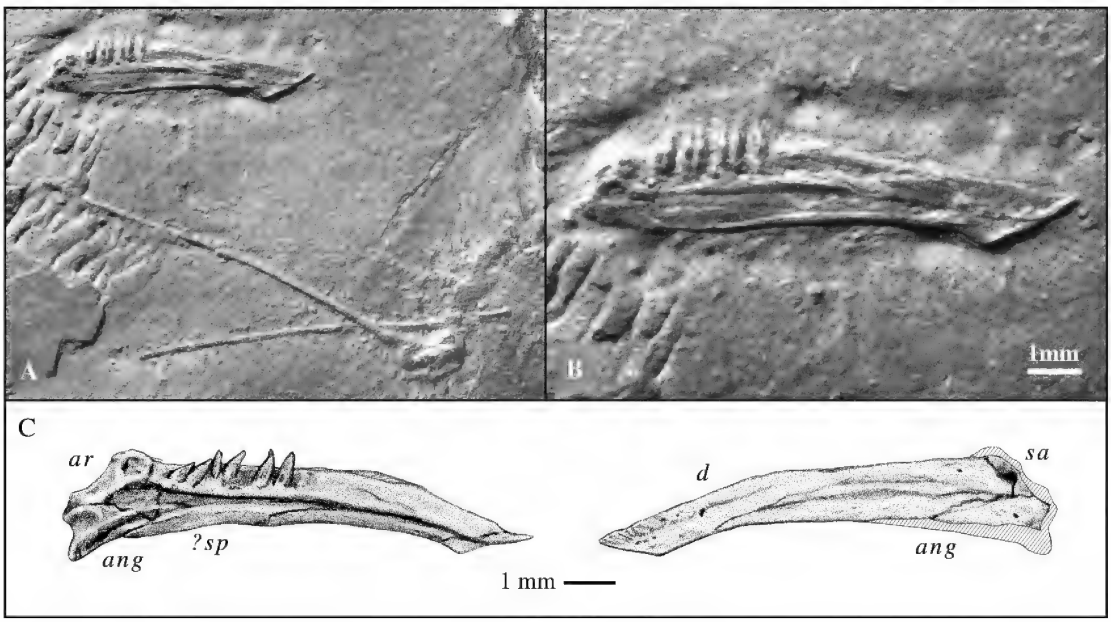


Fig. 8. Mandibles of *Hypuronector*: **A,** AMNH 2080, left mandible, medial view and associated caudal vertebrae from Granton Quarry; **B,** close up of mandible in A.; **C,** YPM 56388, lateral and medial views of negatively prepared specimen. Abbreviations are: *d,* dentary; *ang,* angular; *ar,* articular; *sa,* surangular; *?sp,*? splenial. Photograph by P. Olsen.

VERTEBRAE: The presacral vertebrae in the holotype are somewhat scattered, and some are missing because of damage to the slab prior to collection (fig. 6). Thirteen vertebrae are present anterior to the tail. Among these are three articulated cervical vertebrae seen in ventral view and another anterior cervical vertebra, poorly preserved. There are five rather poorly preserved vertebrae in the middorsal region, two of them in anterior aspect with ribs attached. In the posterior dorsal area are more vertebrae, one with a fairly complete centrum, the other with the centrum largely destroyed. The vertebra with the centrum preserved is visible in lateral view, and has a rather tall neural spine. It may be from the posterior section of the presacral series. The other vertebra, in front of the one just described, has a strong transverse process suggesting that it may be a dislocated sacral.

The holotype shows 38 caudal vertebrae in close articulation (the first two slightly displaced), each with a long chevron or hemal spine. In front of the first of these vertebrae, which has a comparatively short but stout chevron, there are three vertebrae that lack chevrons. The last of these has very stout transverse processes, indicating the possibility that it and its two fellows may be sacrals. However these three vertebrae may be anterior caudals since the first two or three caudals following the sacrum usually lack chevrons, as an accommodation for the exit of the cloaca. Therefore it is possible that the caudal count may be as high as 41 or even slightly more, assuming that a few very small, delicate vertebrae may be missing from the tip of the tail.

The first three articulated vertebrae, which almost certainly are cervicals, appear to have narrow ventrally constricted centra, and broad neural arches with the zygapophyses laterally widely spaced. Short, broad processes extend laterally for the attachment of cervical ribs that might have been essentially holocephalous. Comparison with the cervical vertebrae of other drepanosaurids is hampered by lack of preservation in *Drepanosaurus* and *Dolabrosaurus,* and preservation in lateral view in *Megalancosaurus,* however, they appear shorter in *Hypuronector* than

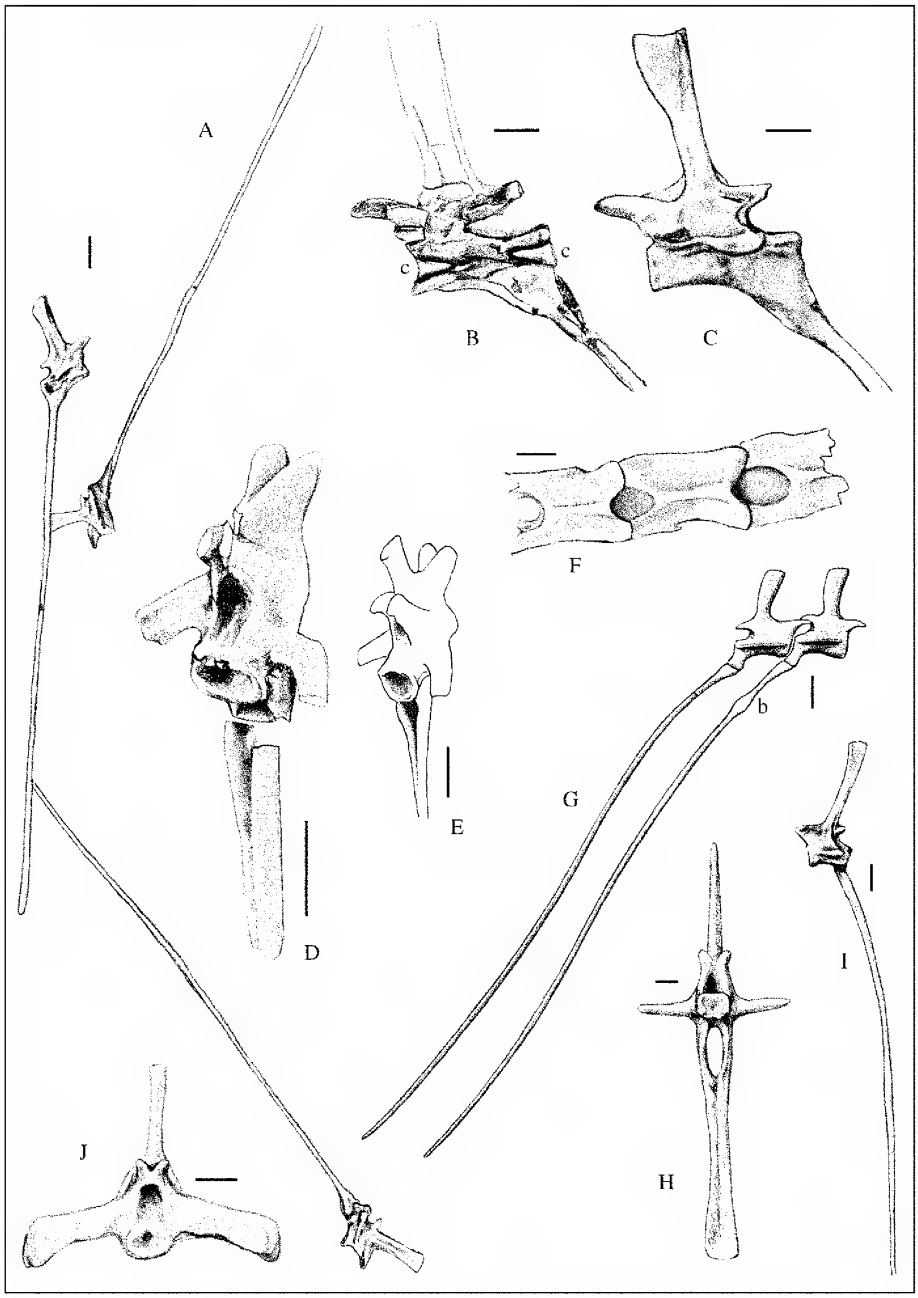
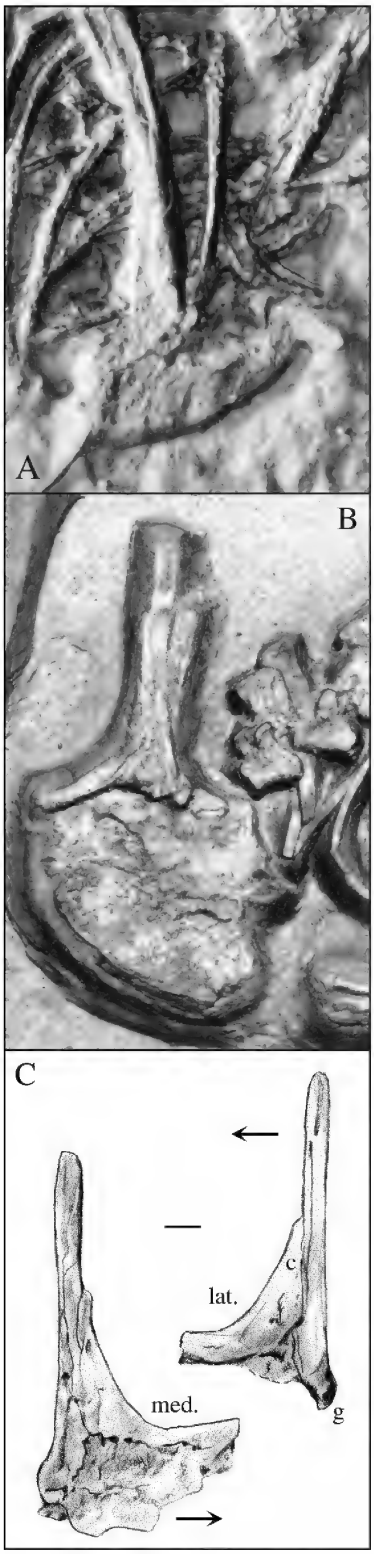


Fig. 9. Examples of vertebrae of *Hypuronector* (scale bar 1 mm): **A,** three associated caudal vertebrae with chevrons (YPM 56390); **B,** early stages of negative preparation of caudal vertebra and partial chevron (YPM 56389) showing matrix filling notochordal cones (c), shown reversed; **C,** same vertebra as B, fully prepared; **D,** negatively prepared, obliquely preserved caudal vertebra and partial chevron (YPM 56391); **E,** reconstruction of specimen in D; **F,** three cervical vertebrae in dorsal view (AMNH 7755); **G,** two successive caudal vertebrae and chevrons from the holotype (AMNH 7759); **H,** proximal caudal vertebra and chevron in anterior view (YPM 8641); **I,** isolated caudal vertebra and chevron (YPM 56387); **J,** isolated sacral vertebra in anterior view (YPM 56392).



in the latter genus. The neural spines of the cervicals appear low as in *Megalancosaurus.*

Anterior dorsal vertebrae are seen in lateral view in AMNH 1721 (fig. 7). As in other drepanosaurids these vertebrae are tall, with prezygapophyses extending far in advance of the centrum. However unlike *Drepanosaurus* or *Megalancosaurus,* the neural spines are clearly not massively expanded.

The single vertebral centrum visible in the holotype in the middorsal region is somewhat elongated, ventrally constricted, and amphicoelous, as are the vertebrae in the same region in AMNH 1721 (fig. 7). This is also true of the vertebra in the posterior dorsal region, seen in lateral view. A single sacral vertebra from Weehawken (YPM 56392) is preserved in anterior view (fig. 9).

The details of most of the presacral vertebrae are at best rather uncertain; it is therefore fortunate that the caudal series, in nice articulation in the holotype, affords a more satisfactory view of the vertebral structure in this little reptile (fig. 6). In the caudal series the vertebral centra are comparatively heavy in the anterior part of the tail, but they become more slender and somewhat more elongated in progression from front to back, as might be expected. The last vertebra present is very small, but there may have been two or three additional vertebrae—so small and fragile as to escape preservation. The neural spines in the anterior part of the tail are very tall and slender, the tallest equivalent in length to the articular three caudals in this section of the tail. The spines become progressively shorter and heavier toward the back of the tail so that in the last dozen or so vertebrae the spines are shorter than the length of their respective centra. The first few caudal vertebrae have strong transverse processes, but these quickly decrease in length and thickness to become rather thin, short

←

Fig. 10. Shoulder girdle of *Hypuronector* (scale bar 1 mm): **A,** AMNH 7759 (anterior is to right); **B,** AMNH 1721 (anterior is to left); **C,** right scapula and ?clavicle, YPM 56386 (lat., lateral view; med., medial view; g, anterior part of glenoid fossa; c, ?clavicle; arrow points anteriorly). Photographs by Chester Tarka.

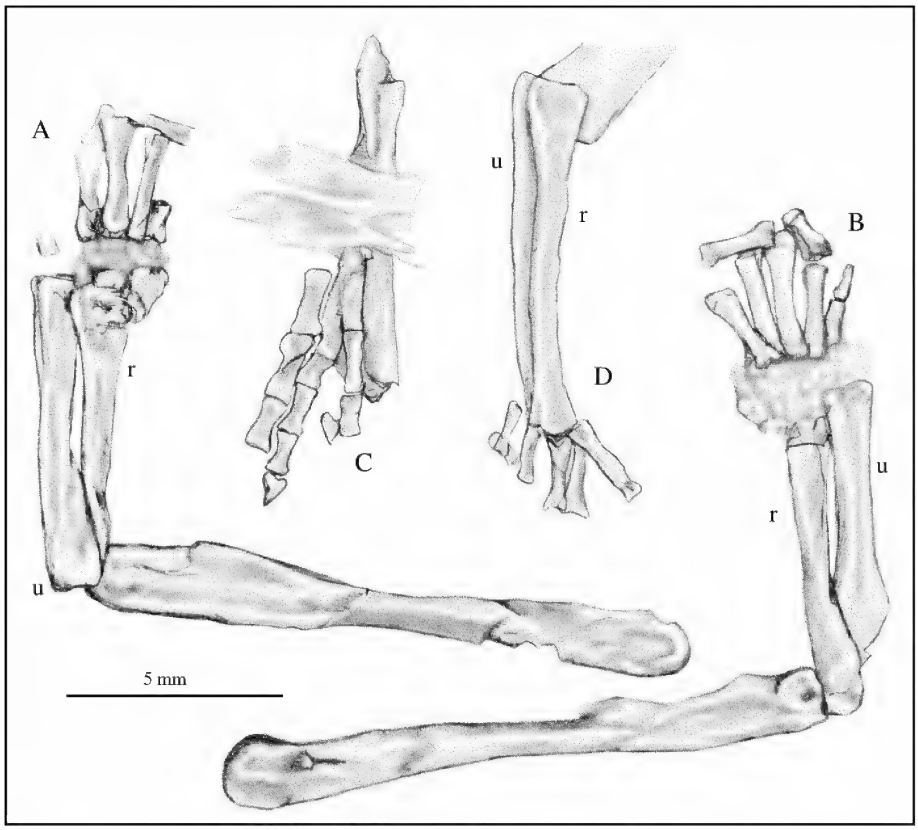


Fig. 11. Forelimb of *Hypuronector.* **A** and **B,** YPM 56393, isolated forelimb drawings of part and counterpart slabs. **C** and **D,** AMNH 7759, forelimbs: (C) left manus, radius, and ulna and (D) right manus, radius and ulna. Identification of radius (r) and ulna (u) is not certain.

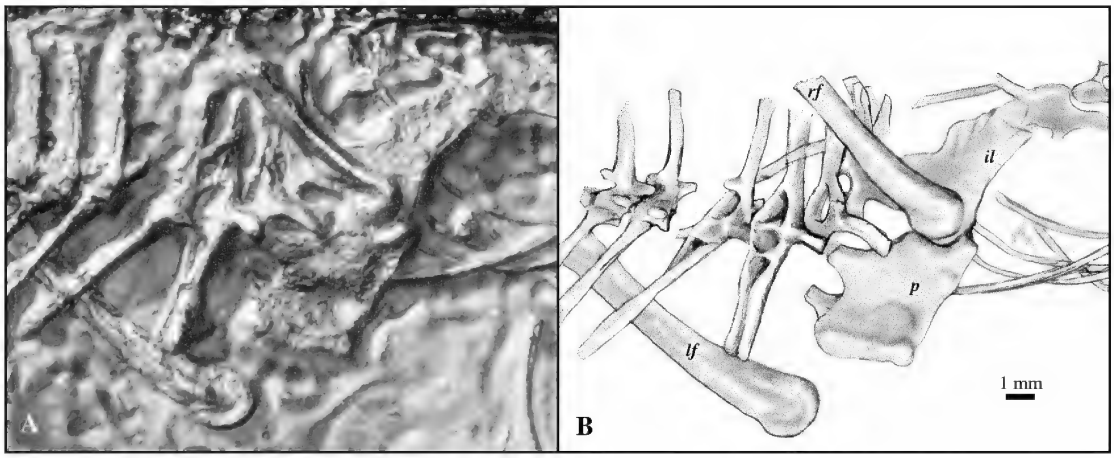


Fig. 12. Pelvic girdle of *Hypuronector*; photograph (**A**) and drawing (**B**) of AMNH 7159. *p,* pubio-ischiatic plate; *il,* ilium; *lf,* left femur; *rf,* right femur. Photograph by Chester Tarka.

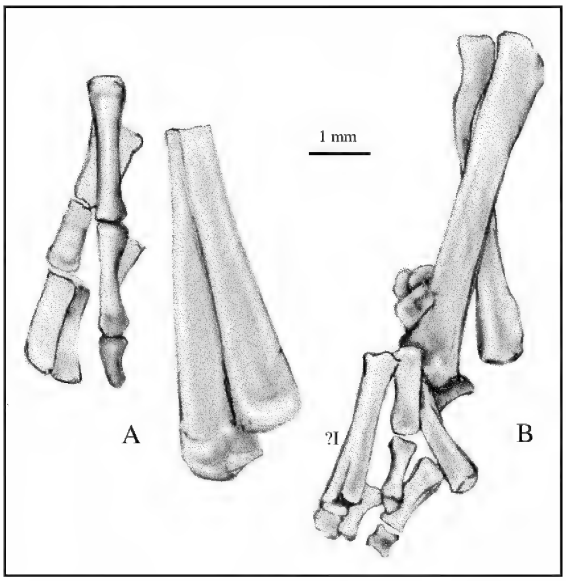


Fig. 13. Distal parts of the hind limb of *Hypuronector*. **A,** left hind limb; **B,** right hind limb. ?I, is possible proximal phalanx of digit I.

blades in most of the vertebrae. Details of the caudal vertebrae can be best seen in the Weehawken material (fig. 9).

At least some of the vertebrae have remnants of the notochordal canal, as observed the caudals. This was evident during progressive acid digestion of the isolated caudals of YPM 56389 in which the natural casts of the notochordal cones could be clearly seen (fig. 9).

The distinctive feature of the tail in this reptile is the elongated chevrons or hemal spines, already mentioned. As has been pointed out, the first three vertebrae at the front of the caudal series lack hemal arches. The next vertebra, however, has a very strong chevron, only slightly longer than the neural spine, and anteroposteriorly expanded in its distal part. This chevron is in marked contrast to the one on the next succeeding vertebra, which is slender and straight and notably longer than the neural spine above it. The next two chevrons are successively longer and slightly expanded distally. The following chevron, still longer, is curved forward in its distal half, but the end is not expanded. From here on back the chevrons are progressively longer, reaching a maximum in about the mid-section of the tail, from which region they decrease to some degree posteriorly. However, even the most posterior chevrons are relatively long. As noted in the diagnosis, the longest chevrons are about equivalent to the length of 11 articulated caudal vertebrae. All of these hemal arches are extraordinarily slender. The most anterior chevrons are slightly inclined back from a vertical position, but in the progression back along the tail they become increasingly inclined until the most posterior ones are at very acute angles with the centra to which they are attached. The chevrons are attached at the very back of the centra.

In about 18 chevrons within the middle and posterior section of the tail of the holotype specimen there is a swelling in the bone at a distance below the centrum about equal to or slightly greater than the length of the neural spine. In at least two of the chevrons it appears that a joint or articulation is present within this swelling between the short proximal and the long distal sections of the bone, which is to some degree reminiscent of the elongation of the neural spines in certain pelycosaurs. As none of the other specimens referred to *Hypuronector* show these types of joints (fig. 9), they are probably pseudoarthroses caused by damage and healing during the life of individual.

It should be added that AMNH 7205 from Granton shows a virtual identical development of the anterior caudals with their attendant chevrons as is seen in the holotype. Moreover, the specimen from Weehawken (YPM 56387), a single vertebra, is closely comparable to anterior caudal vertebrae in the holotype, except that it has a very long chevron (fig. 9). This leads us to suspect that the anterior chevrons of the holotype, behind the fifth in the series, are incomplete, as indeed is indicated in several instances by grooves in the matrix where bones once were present. Chevrons are elongate in drepanosaurids in general; however, they are extremely so in *Hypuronector*. In fact, they are proportionally longer in this new form than any other known tetrapod, and are the principal evidence for its aquatic mode of life (see below).

Ribs: The ribs of *Hypuronector* are long and strongly curved, particularly in the mid-

dorsal and posterior dorsal region. It is evident from the shapes of these ribs that the thorax was capacious. The anterior ribs are somewhat shorter and heavier than those in the more posterior region of the trunk. In these anterior ribs the capitulum and tubercle are distinctly separate from each other, but in the more posterior, slender ribs the two structures become functionally holocephalous. Because they remain in position relative to the vertebrae even upon disarticulation, it clear that the dorsal ribs are fused to the centra (fig. 6), which is nearly the exact condition in *Dolabrosaurus* (Berman and Reisz, 1992: fig. 1). Ribs are similarly fused to at least the distal dorsal vertebrae in *Megalancosaurus.* In *Drepanosaurus,* there seems to be a clear, very thin groove separating the ribs from all of the dorsal vertebrae. However, the rotation of the most of the centra with the ribs in articulation suggests that the ribs were very tightly attached, if not in fact fused.

PECTORAL GIRDLE: The pectoral girdle is represented in three specimens (the holotype, AMNH 1721, and YPM 56386). A scapula and coracoid are definitely present and evidently tightly attached (figs. 6, 7, 10). The scapula is very unusual and very similar to that of *Megalancosaurus*; it is very elongate and rod-shaped. It appears to bear the dorsal edge of the glenoid fossa.

The coracoid appears more or less oval. However, it appears to have been fused to its opposite along the midline and, because of crushing, its ventral margin is greatly obscured. A crescent-shaped structure is attached to the anterodorsal juncture of the scapula and coracoid. It could be a clavicle. The bone is rather short and curved, its distal end coming to a blunt point. The surface of the bone is flattened. In its general aspects this bone resembles the clavicle in a modern lizard, or the same bone in *Macrocnemus* as figured by Peyer (1937, fig. 22). According to Renesto (1994a, 1994b) clavicles are absent in *Drepanosaurus.* however, they could still be firmly fused to the scapulacoracoid, and Renesto (2000) reports them in new specimens of *Megalancosaurus.*

A small three-dimensional shoulder girdle has recently been recovered from one of the *Coelophysis* blocks from the Chinle Formation of Ghost Ranch, New Mexico (GR1113; Jerald Harris and Alex Downs, personal commun., 1999). It shares with other drepanosaurids, including *Hypuronector,* long rod-like scapulae and may be an uncrushed version of a drepanosaurid shoulder girdle. This specimen shows that the drepanosaurid shoulder girdle was unusually robust and quite complex in shape.

FORELIMB: The humerus is long, slender, and straight; considerably longer than the radius and ulna (figs. 6, 13). Distally it is somewhat expanded, and probably was even broader at its proximal end, but unfortunately the head of the bone in the holotype is not present in one humerus, and in the other is buried under other bones and therefore not visible. Some additional detail can be seen in the isolated humerus from Weehawken (YPM 56385). The radius and ulna are straight bones, and almost equal in size and about two-thirds the length of the humerus. They compare with the same elements in *Megalancosaurus* as figured by Renesto (1994b) in general aspects and proportions. An isolated long bone from Weehawken (YPM 56386) shows a distal concavity at the? posteroventral margin of the bone like that on the humerus of *Megalancosaurus.* Renesto (1994b) described a fossa for the olecranon on the ulna. Poor preservation obscures the distal ends of the ulna in the holotype of *Hypuronector,* however. It is possible that the crushed condition of the bones is a consequence of being hollow in *Megalancosaurus* as described by Renesto (1994b).

The isolated right manus is in partial articulation, with some of the phalanges missing in the holotype (fig. 11). The carpus is hidden by the three articulated anterior presacral vertebrae. The left manus is in position at the distal end of the left radius and ulna, but is very incomplete. Individual carpal bones are not distinguishable. There are five digits seen in the right manus, with elongated metacarpals. The first metacarpal, somewhat shorter than the other four, is also much heavier than the others. The remaining metacarpals are comparatively slender, and the fifth member of the series, although somewhat shorter than metacarpals II–IV, is nevertheless an elongated bone. It is possible that some of what we are interpreting as

metacarpals are actually elongate proximal carpals, like those present in *Megalancosaurus.* The proximal phalanges are large and elongated. The ungual phalanx of the third digit in the right manus is small and sharply pointed. Given the large variation in phalangeal formulas in drepanosaurids and the poor preservation of the manus in *Hypuronector,* the phalangeal formula remains conjectural. The manual preungual phalanx does not appear to be longer than that preceding it, as is the case in *Megalancosaurus* and *Drepanosaurus.*

Pelvic Girdle: The right side of the pelvis is present in the holotype, with the femur in articulation (figs. 6, 12). The ilium is unusually deep and rather abbreviated anteroposteriorly, but anterodorsally expanded, much reminiscent of some very much larger therapsids (e.g. dicynodonts). Its very unusual shape is virtually identical to that seen in *Megalancosaurus* and similar to *Drepanosaurus.* The posteroventral edge of the ilium is covered by the femur. The pubis and ischium are coalesced to form what seems to be an uninterrupted puboischiadic plate. The anterior termination of the acetabular border of the pubis is expanded into a knoblike peduncle for articulation with the ilium. An obturator foramen, like that described in *Megalancosaurus* by Renesto (1994b), is not obvious but could easily be obscured by preservation and preparation. The ischium of *Hypuronector* appears to have a prominent posteriorly projecting process along its posterior edge that seems similar to a less pronounced process in *Drepanosaurus* (Pinna, 1984; Renesto, 1994a).

Hind Limb: As seen in the holotype, the femur is a long, straight, slender bone, almost exactly equal in length to the humerus (fig. 6). There is very little flexion in the shaft of the femur, and the well-rounded head is only slightly offset from the axis of the shaft. The disparity in length between the femur and the tibia is even greater than that between the upper and lower elements of the forelimb, for the tibia and fibula are only half the length of the femur. These two lower bones are rather stout and approximately equal in diameters. In general proportions these hind limb elements are similar to, but more slender than, those of *Megalancosaurus* and *Drepanosaurus.* The arms are thus longer than the legs.

The pedes are very incomplete and very difficult to interpret (fig. 13). The tarsals are very poorly preserved. A rather heavy metatarsal or proximal phalanx is visible in the left pes, about equal in length or perhaps slightly longer than the first metatarsal (fig. 13). It appears to have an unusual shape distally, perhaps suggestive of but less extreme than the proximal phalanx of digit I in *Megalancosaurus* (Renesto, 1994b). Three elongated phalanges are present, and the distal part of another metatarsal can be seen with its upper end hidden by the more proximal of the two articulated phalanges. Beyond this little can be said about the pes in *Hypuronector.* As for the manus, the pedal phalangeal formula is unknown.

RELATIONSHIPS

Hypuronector is a very strange little tetrapod. It possesses a variety of odd characters and incompleteness in crucial areas (e.g., the skull) that make it very hard to place in known groups. When it was first found in the 1970s and early 1980s we were not even certain it was an amniote, and if it was an amniote, whether it was a saurian or synapsid. However, the more recently described *Megalancosaurus, Drepanosaurus,* and *Dolabrosaurus* share some of the peculiar features seen in *Hypuronector* and permit at least a sketchy phylogenetic analysis (fig. 14), for which we consider *Petrolacosaurus* as an outgroup (Peabody, 1952; Reisz, 1977).

Hypuronector, Megalancosaurus, and *Drepanosaurus* share the following characters, which we regard as synapomorphies (numbers refer to fig. 14): (1) caudal vertebrae with anteroposteriorly elongated bladelike transverse processes through most of tail and with prezygapophyses of proximal caudals extending anteriorly well beyond centrum and postzygapophyses extending posterodorsally from neural spine base; (2) vertebrae with zygophyseal facets generally set very close to midline in postcervicals; (3) neural spines unusually long, especially on caudal vertebrae; (4) dorsal ribs firmly attached to centra; (5) hemal arches or chevrons fused to posterior part of anterior three-

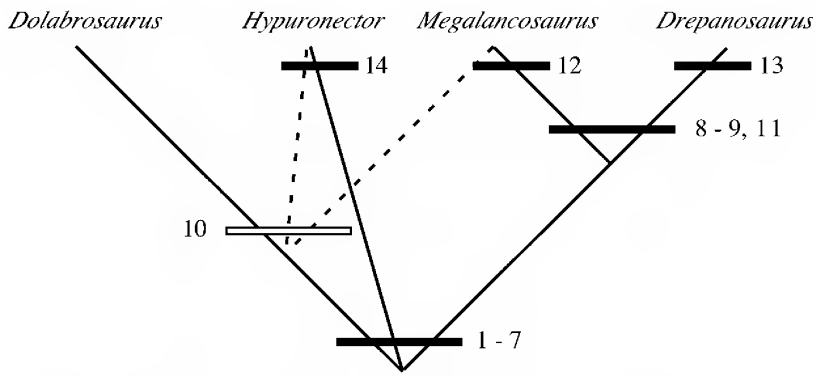


Fig. 14. Tentative cladogram of relationships within Drepanosauridae. Characters are: 1, caudal vertebrae with anteroposteriorly elongated, bladelike transverse processes through most of tail and with prezygapophyses of proximal caudals extending anteriorly well beyond centrum and postzygapophyses extending posteriodorsally from neural spine base; 2, postcervical vertebrae with zygophyseal facets generally very close to midline; 3, neural spines very long, especially on caudal vertebrae; 4, dorsal ribs firmly attached to centra; 5, hemal arches or chevrons fused to posterior part of anterior three-quarters of caudal vertebrae and much greater in depth than height of the neural spines; 6, pectoral girdle with high and rodlike scapula; and 7, pelvic girdle with high, anteriorly directed blade of ilium. 8, Bifurcate or fenestrate chevrons; 9, distinctly enlarged and modified neural spines in shoulder region; 10, dorsal ribs fused to centra; 11, reduced manual and pedal phalangeal formula; 12, "opposable" digit I on pes; 13, giant ungual phalanx on manual digit II; 14, extremely deep tail. Note that *Dolabrosaurus* has no apparent unique derived characters. Dotted lines indicate less favored relationship indicated by character 10.

quarters of caudal vertebrae and much greater in depth than height of the neural spines; (6) pectoral girdle with high and rodlike scapula; and (7) pelvic girdle with high, anteriorly directed blade of ilium. These characters are also present in *Dolabrosaurus,* with the exception of the ilium, which is not preserved in the latter form. Together these characters comprise the synapomorphies of the Family Drepanosauridae, as summarized in the family diagnosis, above.

Within the Drepanosauridae, *Megalancosaurus* and *Drepanosaurus* differ from *Hypuronector* and *Dolabrosaurus* in sharing: (8) bifurcate or fenestrate chevrons anteriorly; and (9) a distinct enlargement and modification of the neural spines in the shoulder region. These bifurcate or fenestrate chevrons are definitely absent in both *Hypuronector* and appear absent in *Dolabrosaurus,* which we take to display the primitive condition. *Hypuronector* definitely lacks the enlarged neural spines of *Megalancosaurus* and *Drepanosaurus,* again presumably primitively. The shoulder region is not preserved in *Dolabrosaurus.* Another additional synapomorphy of *Megalancosaurus* and *Drepanosaurus* may be a pair of elongated proximal carpals, identified as ulnare and intermedium by Renesto (1994a, 1994b). However, the lack of preservation of this region in *Hypuronector* and *Dolabrosaurus* makes this character problematic.

Hypuronector, Megalancosaurus, and *Dolabrosaurus* share posterior dorsal ribs that are clearly fused to the centra, which we assume is a derived condition (character 10). This is the only derived character shared between these latter two taxa to the exclusion of *Drepanosaurus,* and we regard the difference as weak evidence of relationship, because it could easily be ontogenetic. *Megalancosaurus* and *Drepanosaurus* share a reduced phalangeal formula in the manus and pes (character 11) compared to the primitive diapsid condition (e.g., *Petrolacosaurus*). The pes of *Megalancosaurus* is very modified with a very peculiar "opposable" digit I (character 12). The pes of *Drepanosaurus* lacks this feature, and possesses a more normal digit. The manus of *Megalancosaurus* and *Drepanosaurus* is divergently modified,

with a more reduced phalangeal formula and giant ungual phalanx on digit II (character 13) in the latter (Renesto, 1994a) and apparently oppositely oriented digits in the former. Because the manus and pes are incomplete in *Hypuronector* and *Dolabrosaurus,* it is not known if the reduced phalangeal formula of *Megalancosaurus* and *Drepanosaurus* is a synapomorphy of just the two latter genera or a synapomorphy of the Drepanosauridae. A character of the tail possibly indicating that *Dolabrosaurus, Megalancosaurus* and *Drepanosaurus* are more closely related to each other than to *Hypuronector* is the tendency of the tails of all three of the former genera to curl ventrally, while that of *Hypuronector* is straight. However the curling of the tail may be taphonomic and we regard this character as very weak, especially for *Dolabrosaurus.* Although all drepanosaurids have a relatively deep tail, that of *Hypuronector* is uniquely deep among amniotes (character 14).

An additional small reptile from the Norian of northern Italy (MCSNB 4751) is certainly a drepanosaurid and appears to be similar to *Megalancosaurus,* but a distinct taxon (Renesto, 2000). The specimen, under study by Rupert Wild, retains several primitive characters compared with *Megalancosaurus and Drepanosaurus,* including a proportionally shorter neck and less modified chevrons (Renesto, personal commun., 1999). When described in detail, MCSNB 4751 should provide tests of the relationships hypothesized above.

Drepanosauridae was erected without description or diagnosis by Olsen and Sues (1986). The name was used again by Carroll (1988) and finally described and diagnosed by Berman and Reisz (1992). As described by Berman and Reisz (1992), the Drepanosauridae, is explicitly intended to include *Drepanosaurus* and *Dolabrosaurus* while the family Megalancosauridae Renesto, 1994b, was intended to include only *Megalancosaurus.* Drepanosauridae has priority over the family Megalancosauridae, and as defined by Berman and Reisz (1992) and modified here, Drepanosauridae is the more inclusive group. However, if additional material and analysis should prove *Drepanosaurus* and *Megalancosaurus* more closely related to each other than to either *Hypuronector* or *Dolabrosaurus,* as suggested here, then the Megalancosauridae would be an appropriate moniker for the group and the Drepanosauridae could be raised to a higher rank.

Assuming that *Hypuronector* is correctly placed within the Drepanosauridae and that the family is a monophyletic group, it is clear from the skull of *Megalancosaurus* that the family is a member of the Diapsida of the Reptilia. If *Megalancosaurus* has an antorbital fenestra as suggested by Calzavara et al. (1980), it is also a member of the Archosauriformes. However, the presence of an antorbital fenestra is far from certain (Renesto, 1984b) and a mandibular fenestra, an archosauromorph synapomorphy, appears absent in both *Hypuronector* and *Megalancosaurus.* Thus, for the present, we regard *Hypuronector* as a drepanosaurid within the Diapsida and possibly within the Archosauriformes. By our analysis it is not a lepidosauromorph, and there is certainly nothing but the most superficial similarities suggesting relationship to birds (contra Feduccia and Wild, 1993).

MODE OF LIFE

Hypuronector has a very deep tail, superficially comparable in shape to that of gymnotid or gymarchid fishes (figs. 6, 15). No other tetrapod has such elongate chevrons, or a tail with a strongly similar structure. The similarity at least superficially to the deepened tails in aquatic tetrapods such as newts and crocodilians, however, strongly suggests that the tail of *Hypuronector* was adapted for sculling in water. An aquatic habit is in keeping with the taxon's relative abundance at Granton Quarry and Weehawken, where it is considerably more common than the other small aquatic reptile present in the same beds, *Tanytrachelos.* The limbs, however, are relatively quite long. This may have been compensation for the great depth of the tail, which would otherwise interfere with terrestrial locomotion. There is no evidence that *Hypuronector* could lift its tail so that it was at an acute angle to the dorsal series; all of the articulated specimens found thus far have the caudal series in line with the dorsal vertebrae. Thus, it appears unlikely that it could

have been a balancing organ for arboreal life, as might be suggested by its relationship with *Megalancosaurus* and *Drepanosaurus.* Evidently, *Hypuronector* had a beak anteriorly, as judged from the pointed but toothless anterior mandible, the functional significance of which is obscure.

The aquatic mode of life, inferred here for *Hypuronector,* differs from that inferred for the other drepanosaurs known from relatively complete remains, specifically *Megalancosaurus* and *Drepanosaurus,* which have been interpreted as arboreal (Renesto, 1994a; Ruben, 1998) or fossorial (Pinna, 1984). *Megalancosaurus* possesses manual and pedal structures compatible with grasping of tree branches and insectivory (Renesto, 1994b; Ruben, 1998), and *Drepanosaurus* has massive claws that Pinna (1984) interpreted as digging adaptations, but Renesto (1994a) interpreted as devices for bark scraping. In any case, drepanosaurids show a surprising amount of structural diversity, certainly suggesting different and varied modes of life.

TEMPORAL RANGE OF THE DREPANOSAURIDAE

Drepanosaurus is known from the marine Middle to Late Norian age Calcare di Zorzino and the Argillte di Riva di Solto of northern Italy (Renesto, 1994b). *Megalancosaurus* is also known from the Calcare di Zorzino as well as from the Norian marine "Dolomia di Forni" of northern Italy (Renesto and Paganoni, 1995). *Dolabrosaurus* is from continental strata of the middle Upper Petrified Forest Member of the Chinle Formation of north-central New Mexico and is of Early Norian age (Berman and Reisz, 1992). *Hypuronector* is from the lacustrine Lockatong Formation of Late Carnian age. Using the time scale of Kent and Olsen (1999) and Olsen and Kent (1999), the numerical age of *Hypuronector* is about 222 Ma (age of the Nursery and Ewing Creek members) (fig. 2). The age range, using the same time scale, of the Italian material is about 208 to 213 Ma and that of *Dolabrosaurus* 213–218 Ma. The Drepanosauridae thus span a minimum duration of about 208–222 Ma or about 14 million years. Given the very derived nature of *Hypuronector* and that

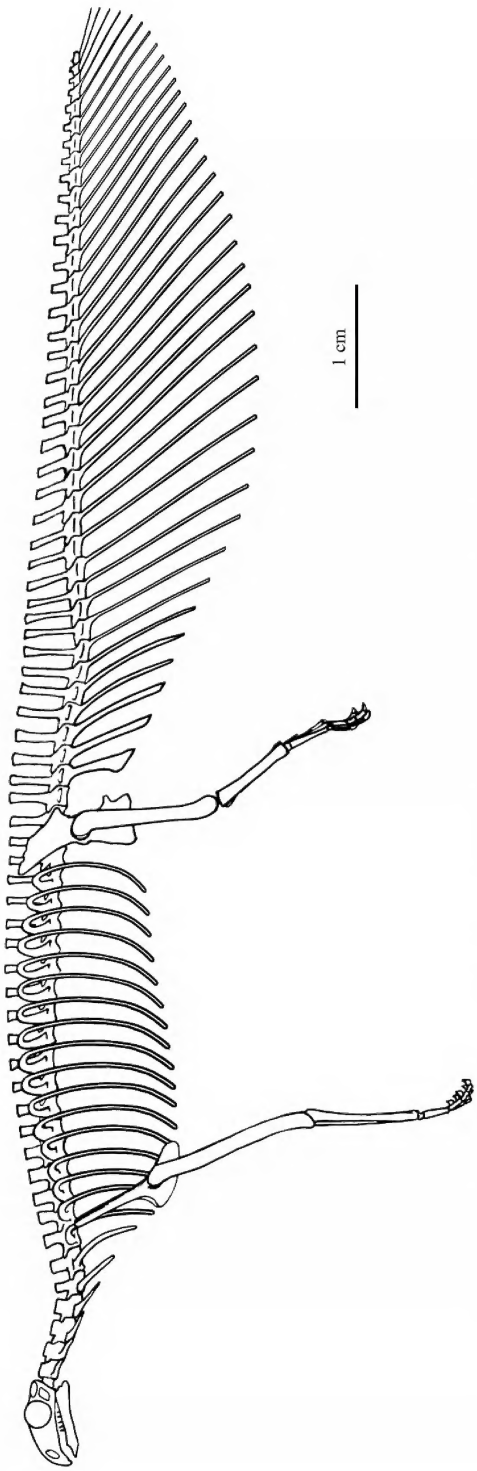


Fig. 15. Reconstruction of *Hypuronector.* The cranium and number of cervical vertebrae are conjectural.

of the rest of the diversely specialized drepanosaurids, the family is presumably at least several million years older.

CONCLUSIONS

Hypuronector was a small, aquatic reptile belonging to the family Drepanosauridae. It has deep tail comprising uniquely elongated chevrons and high neural spines and an anteriorly edentulous mandible. It is a member of a remarkably structurally and presumably trophically diverse family with arboreal, possibly fossorial, and aquatic members. *Hypuronector* is the oldest known member of the family (Late Carnian) with representatives surviving to at least the middle Norian, a span of minimally 14 million years. Given their manifold trophic specializations, and very large geographic area over which the Drepanosauridae are known to have lived (western US to Italy), they represent an unexpectedly significant and diverse component of Late Triassic ecosystems, until recently unknown.

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